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HISTORICAL PERSPECTIVES IN ECOLOGY AND EVOLUTIONARY BIOLOGY: The Use of Phylogenetic Comparative Analyses

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Abstract

Hypotheses about the adaptive significance of a trait have long been tested by making comparisons among species. Many recent studies emphasized that conclusions about the origin and maintenance of adaptations as well as the underlying selective processes derived from comparative tests may be strengthened with the inclusion of a phylogenetic hypothesis. Major advances in the comparative approach have therefore occurred with the coincident developments in numerical methods available for phylogenetic inference. In this review, we outline the advantages and possible disadvantages of adopting an historical approach in ecological and evolutionary studies. We begin by discussing the need for including information on the phyletic relationships among taxa in ecological and evolutionary analyses. Next we describe how an historical approach not only refines the definition and recognition of adaptations, but also provides an objective definition of "phylogenetic constraints." Because conceptual and analytical advances in comparative methods are occurring quite rapidly, we provide a brief summary of the goals,

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assumptions, and potential applications of the various methods presently available to biologists. Finally, the relative performance of various comparative methods is discussed as well as the problems inherent in choosing a well-supported phylogeny and the potential weaknesses inherent when using taxonomic classification instead of a phylogenetic tree. Current phylogenetic trees are testable hypotheses, and the conclusions emanating from recent comparative analyses should be considered tentative. Our interpretations regarding the adaptive significance of a character may be subject to retesting or revisions as additional data regarding a trait complex are collected and the available phylogenetic hypotheses are refined.

INTRODUCTION

The description and explanation of diversity in the natural world are major goals in organismal biology. An accepted tenet has been that adaptation to local, extrinsic selective conditions represents the genesis of the spectacular variety of life. For a number of years, ecological and evolutionary studies often adopted a nonhistorical approach to unravel the causal mechanisms of diversity (see reviews in 16, 73, 80, 97, 98, 135, 136). Comparisons drawn from a broad range of taxa served either to generate or to test hypotheses concerning the functional significance and evolution of adaptations. Individual species often comprised the independent data points to determine correlations between an environmental factor, such as habitat type, with a trait and its biological role, e.g. femoral length and running performance. Statistically significant correlations usually suggested evidence for the adaptive significance of a trait. Because all traits were assumed to embody adaptive solutions to contemporary environmental conditions, ecologists and evolutionary biologists had to make a judicious choice of taxa to demonstrate a selective scenario.

The dependence on correlational evidence and the assumption that extrinsic selective processes were largely responsible for shaping the form of a phenotypic trait have been thoroughly discussed as weaknesses of nonhistorical comparative analyses (32, 33, 71, 73, 89, 97, 100, 185, 186). The absence of an explicit historical perspective weakens the conclusions from comparative analyses. Delineating the causal basis underlying the origin or variance of a trait may be ambiguous, for the manifestation of phenotypic traits in extant species may reflect phyletic heritage rather than adaptation to recent local environmental features. For example, the widespread occurrence of a morphological trait in association with a particular ecological characteristic may either represent repeated and independent evolutionary events because of common selective factors or an instance of inheritance from a common ancestor (4, 6, 16, 21, 24, 30, 32, 61, 82, 165, 186). Although once

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considered unimportant relative to contemporary selective factors, historical explanations of ecological and evolutionary phenomena are now becoming an integral component of comparative analyses (16, 80).

A number of authors reiterate the point that species within a monophyletic clade are part of a nested hierarchy of relationships and should not be used as independent data points in conventional statistical analyses for a variety of reasons (17, 23, 24, 52). The most critical feature is the inefficiency of some nonhistorical statistical analyses to account for the correlation among species attributable to phylogeny. A failure to consider phylogeny increases the likelihood of obtaining inflated estimates of the number of independent origins of a trait and may favor an adaptive explanation (32, 33, 52, 61, 89, 155). As a result, correlations among traits derived from species values may be unreliable (111, 120). Consider the evolution of viviparity in the lizard genus *Sceloporus*. Over 28 of the 68+ species are viviparous (175). Guillette et al (78) compared mode of reproduction with environmental, geographic, and other life history variables in an attempt to determine the evolution of viviparity. Their study used each species of *Sceloporus* as an independent data point in a series of contingency table analyses. Such analyses favored the interpretation that current life history patterns represent adaptations to contemporary environments. However, in a taxonomic survey of the distribution of viviparity, Shine (169) found between four and six independent origins within *Sceloporus*. An analysis based on the phylogeny of *Sceloporus* derived from karyotype data (175) showed that viviparity probably arose at least three times (DB Miles & DN Reznick, unpublished). Mapping the distribution of viviparity onto a phylogeny demonstrated that fewer data points were actually available for a statistical analysis. Consequently, alternative methods are necessary for elucidating the antecedent environmental and life history variables associated with the evolution of viviparity in *Sceloporus*.

The addition of a historical perspective to comparative methods has two immediate advantages. First, the addition of a phylogeny has the potential to refine a variety of ecological and evolutionary analyses (e.g. 4, 20, 33, 37, 43, 89, 91, 174). Examples of studies where a phylogenetic approach enhanced an analysis are extensive and range from tests of the adaptive significance of life history traits (e.g. 127) to analyses of ecological character displacement (108). Second, the availability of a phylogenetic tree augments the understanding of how complex structures evolve by suggesting hypotheses of the sequence and direction of character transformations (e.g. 99). However, some disadvantages and limitations are inherent with the use of phylogenies in comparative analyses. Nevertheless, inclusion of a phylogenetic approach may be required in a number of circumstances and should be thought of as a tool that enhances our inferences about ecological and evolutionary patterns.

Comparative methods have been revitalized largely through the coincident

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advances in numerical methods for inferring phylogenies (16, 51, 192) and developments in the statistical procedures that incorporate the influence of history in ecological and evolutionary analyses (16, 21, 60, 61, 76, 80, 113). The result has been an expansion of studies integrating, in various ways, estimates of "phylogenetic relatedness." Any comparative study lacking a phylogenetic perspective now would be incomplete. The availability of a variety of analytical tools in the arsenal of comparative biology allows investigators tremendous flexibility in applying phylogeny to their study. However, the proliferation of new methods and publication of numerous phylogenies for various taxa provide the biologist with several possible analytical options. In light of the rapid developments in the application of historical methods to comparative analyses, our goal is to complement earlier reviews and highlight some recent advances of the field (16, 54, 56, 67–69, 111, 144, 168, 186). The methods for generating phylogenetic hypotheses are beyond the scope of this review and are summarized elsewhere (16, 50, 51, 83, 118, 176, 191, 192). Rather, we assume that a phylogenetic tree is already available. Specifically, we review (i) the need for exploiting phylogenetic information in evolutionary and ecological analyses and the insights that result from the addition of a historical perspective, (ii) goals, assumptions, and application of particular comparative methods, i.e. which method for which question? (iii) the difficulty in choosing well corroborated phylogenies, and (iv) potential biases or weaknesses that may accompany the use of phylogenies. Ultimately, the method of incorporating phylogenetic information in comparative studies depends on the biological question.

THE NEED FOR AN HISTORICAL APPROACH IN ECOLOGY AND EVOLUTION

For over a decade it has been clear that adaptive scenarios generated from comparative studies may be explained by factors other than natural selection, such as phylogenetic conservatism, developmental constraints, and other confounding variables (2, 23, 24, 73, 97, 98, 155, 177, 185). Failure to consider such factors as alternative hypotheses can lead to acceptance of an adaptive explanation when other causal mechanisms may be equally or more probable (e.g. 33, 39, 71, 73, 97, 98). Recently, several major studies emphasized that rigorous testing of ecological, physiological, behavioral, and morphological hypotheses should include a phylogenetic perspective (4, 7, 16, 17, 25, 33, 62, 65, 66, 89, 101, 121, 136, 186).

The utility of including a phylogeny in ecological and evolutionary studies is manifold and has opened a new dimension to any analysis pertaining to the origin and maintenance of complex organismal traits. First, phylogenies may be important in defining and identifying adaptations. Mapping of character

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states onto a phylogeny may provide insights into characters that have evolved uniquely in a single taxon or lineage and represent putative adaptive structures associated with the rapid diversification of a clade (e.g. 46, 86, 92, 101, 122). Second, evidence of adaptations as indicated by convergent and parallel evolution may be inferred from phylogenies. Such studies would benefit from the determination of the characters that have been relatively fixed within a clade and have exhibited evolutionary lability (48). Documentation of ecological convergence in community characteristics has been difficult to establish (see 109, 164). Yet, inclusion of a historical approach, both for choosing the appropriate taxa and for relevant controls, has facilitated a program for the recognition and rigorous testing of convergence (e.g. 13, 109, 121, 153, 164). Third, phylogenetic information may also allow the revision of hypotheses regarding the origin of complex organismal traits and the ecological conditions associated with the evolutionary transformation of specific character states (e.g. 12, 18, 32, 88, 123, 185, 186). Also, hypotheses about the evolution of key factors and novel innovations, which have often been ascribed a causal role in the diversification of clades, may be refined and tested using historical methods (e.g. 101).

Fourth, the direction and magnitude of change may be inferred from the reconstruction of ancestral character states (31, 62, 90, 94). For example, many hypotheses about the evolution of migration in nearctic birds emphasized the advantages in leaving temperate habitats to avoid seasonally unfavorable climatic conditions and exploit milder tropical habitats, i.e. causal inferences were based on contemporary patterns (64). However, recent avian phylogenies suggest that many nearctic migrant species are of tropical origin (103, 172). Therefore, advances in understanding the evolution of migration have occurred by rephrasing the question to ask why tropical birds should leave to breed in the temperate zone (28)? Elaboration of the steps leading to the evolution of long distance migration has been facilitated by comparing ecological attributes of neartic migrants to neotropical species that undergo seasonal migration. Levey & Stiles (103) found that long distance nearctic migrants comprise a subset of neotropical species characterized by altitudinal or intra-tropical movements and similarities in diet and habitat use. Thus, the nearctic migrants may be considered neotropical species that expanded their migratory movements to utilize the seasonally abundant resources of temperate habitats. (28, 103).

Another facet to the union of phylogeny with ecological and evolutionary studies concerns the advances made in conceptual and analytical procedures. The problems inherent with partitioning the "phylogenetic signal" from quantitative traits remains an especially active field of enquiry in comparative biology (e.g. 17, 21, 52, 60, 61, 67, 68, 75, 113, 127, 135). Two issues are relevant to the analysis of phylogeny when using quantitative traits: (i)

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removing the influence of phylogeny in statistical tests, and (ii) the explicit description of variation in a trait due to phylogeny. Concerning the former issue, consider a group of related species of lizards all of which exhibit large clutch sizes. The similarity among the species may be due to descent from a common ancestor or to an adaptive response to prevailing environmental conditions, or to both. Many biologists therefore recognized the need to develop procedures that provide a means for disentangling patterns of variation that represented similar responses to the environment rather than phylogenetic resemblance (21, 113). Such an approach transforms the objective of historical analyses to one of describing trends of variation that represent adaptive scenarios, rather than "effects" or "constraints" attributable to phylogeny (21, 37). Consequently, most of the progress in analyzing quantitative characters in an historical context has centered on the synthesis of statistics and phylogeny. The differences among the recently developed techniques are manifest in the goals of the analysis, the means for integrating phylogenetic information into the statistical procedure, and any assumptions pertaining to underlying evolutionary models of character change (7, 17, 21, 52, 76, 80, 135).

Alternatively, hypotheses about the origin of trait complexes and their functional correlates may be evaluated by tracing the sequence of character transitions directly on the phylogenetic tree (4, 20, 33, 77, 87, 99, 126, 138, 155, 181). Historical reconstructions provide an explicit and testable sequence of the evolutionary transitions leading to the derivation of a complex trait. The historical sequences also illuminate macroevolutionary hypotheses pertaining to the functional significance of a trait that are amenable to testing by experimentation (99, 124). In addition, hypotheses describing particular sequences in the evolution of a trait developed in the absence of a historical approach may be tested by mapping the hypothesized transitions along the branches of a phylogeny (20). Because the appearance of one trait may be contingent on the expression of another, i.e. the possibility of covariation between traits, phylogenies may also be used to describe the correlated evolution of traits (e.g. 115). Unlike the statistical methods that remove the effects of phylogeny, these applications use history to expand our inferences pertaining to the evolutionary transformation of characters within and among lineages (118).

Despite the proliferation of approaches for incorporating phylogenetic information in comparative analyses, a dichotomy has developed between two broad disciplines that espouse specific uses of phylogenies in ecological and evolutionary studies. One school advocates a statistical approach that controls for the confounding influence of phylogeny as a necessary prerequisite in the study of adaptation. Although some controversy exists over which method best removes the influence of phylogeny, a contingent of biologists support

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a particular method as being the "comparative method" (61, 67, 76, 80, 82, 120, 135, 136). These statistical approaches, largely championed by evolutionary ecologists, provide correlative evidence for the relationship between two traits but fail to test explicit hypotheses about the evolutionary change of a trait.

Another group of biologists promotes using the structure of the phylogenetic tree to test specific hypotheses regarding the origin and functional significance of traits and the diversification among clades (e.g. 16, 20, 25, 32, 33, 100). The goals of these studies are the elucidation of character transformation and testing of hypotheses concerning the origin of functional and structural traits. Emphasis is placed on the following methods: out-group analysis to establish character polarity, character optimization, and the development of tests based on sister-group comparisons to determine the adaptive significance of a trait. This focus of character transitions within and between lineages is also known as the historical transformation approach. Rather than circumventing phylogeny, these tests directly include it in the analysis. Not surprisingly, such a difference in philosophy affects the types of hypotheses tested with phylogenetic information. We argue for pluralism in historical analyses, for both statistical and historical transformation methods may be complementary and mutually illuminating.

PHYLOGENETIC INFERENCE IN ECOLOGICAL AND EVOLUTIONARY STUDIES

How can a phylogenetic approach augment the patterns adduced in ecological and evolutionary studies? The information from a phylogenetic tree germane to hypothesis testing includes the characters supporting the branching sequence, character transitions along each branch, homoplasious characters, as well as the topological structure (118, 186, 192). Mapping evolutionary or ecological traits with discrete character states onto the phylogeny will reveal the polarity of the character state transitions and determine whether the trait is plesiomorphic, convergent, or a reversal (20, 26, 33, 58, 126, 159). Character states unique to a single taxon (autapomorphies) or clade (synapomorphies) are possible candidates for hypotheses regarding adaptation and key innovation. Phylogenetic analyses have the ability to reject alternative hypotheses about the origin of such traits, e.g. the chance fixation and subsequent canalization of a character versus the adaptive significance of apomorphic traits. Symplesiomorphies (shared primitive characters) are not informative about hypotheses of adaptation but may provide evidence for the canalization of characters over evolutionary time (161, 163). Whether a trait is found to be derived with respect to an ancestor or to resemble the ancestral state has a profound effect on the types of hypotheses that may be generated

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regarding its origin and functional significance (33, 93, 185). Thus, knowing whether a trait is apomorphic or plesiomorphic will facilitate the choice of characters and controls in the design of a study.

A Phylogenetic Definition of Adaptation

The definition and recognition of adaptation has been a contentious topic in evolutionary biology (3, 5, 6, 14, 23, 24, 55, 73). Although many workers acknowledge the importance of the concept, the controversy involves three critical points: (i) the numerous definitions for adaptation, (ii) the relative importance of confounding variables and intrinsic and extrinsic constraints (23, 24, 55, 73, 97, 98), and (iii) the lack of a quantitative methodology based on evolutionary principles (41). Recent comparative and cladistic methods provide the means for an unambiguous, objective, and testable definition of adaptation. Gould & Vrba (74) revised the definition and identification of adaptation by utilizing an historical perspective. Based on their criteria, an adaptation can be any feature that enhances fitness and whose modification was a result of selection for its current biological role. A trait that has current utility, i.e. exhibits a performance advantage, but which did not result from selection for its present biological role, was designated an exaptation.

Following the advances made by Gould & Vrba (74), the use of an historical approach toward recognizing and defining adaptations has been extended and modified by several recent studies (6, 16, 25, 26, 77, 111, 165, 185). Adopting a phylogenetic framework provides a relatively unambiguous method for distinguishing primitive (plesiomorphic) traits from uniquely derived (autapomorphic) and shared derived (synapomorphic) traits. Furthermore, the use of phylogeny may suggest the types of traits to be analyzed for inferring their adaptive significance as well as the method of investigation. For example, autapomorphies should be investigated in studies that incorporate an optimality criterion (predictions based on biomechanical or optimal allocation models—14), or a microevolutionary approach (covariation between a trait and fitness, sensu 5, 96).

Given a phylogenetic hypothesis, a change in a character state or shift in function coincident with a change in the environment would constitute evidence of adaptation (6, 22, 23). Baum & Larson (6) described a general protocol for discerning adaptations that synthesized and refined a phylogenetically based definition of adaptation. In their description, an adaptation is a trait that must have current utility and that was generated historically through action of natural selection for its current biological role. Losos & Miles (111) summarized the phylogenetic approach to adaptation derived in (6). They noted that the historical approach to adaptation has three features: (i) The

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identification of those lineages in which a trait transformation is evident. This is necessary for the comparison of the historical antecedent state (i.e. plesiomorphic based on outgroup comparison) to the derived state. (ii) Mapping of functional capacity on the phylogeny to determine the transformation sequence for performance. (iii) Determination of the shift in the environment with respect to the genealogical relationships of the taxa as portrayed in the phylogeny. The hypothesized environmental change may correspond with alterations in the "selective regime" experienced by the taxa. The emphasis of this protocol is to delimit the occurrence of shifts in the selective regime, where in the phylogeny the selective regime changed, and whether it is concordant with the transformation of the trait and its function. Appearance of the performance advantage after the evolutionary shift in structure will suggest an exaptation. Adaptations may thus be autapomorphic or synapomorphic but must show a concordant shift in performance. Because the direction of trait change is available, relevant traits that may be adaptations are more easily identified using the historical approach (185, 186).

Studies of Adaptation: A Phylogenetic Criterion for Convergence

Convergent evolution is often presented as evidence of adaptation (57). That is, the appearance of a trait among unrelated species in response to similar extrinsic selection regimes in similar, but spatially distinct habitats (57). In a phylogenetic context, the multiple appearance of a character on different branches of a cladogram also suggests similarity due to independent evolution rather than ancestry (16, 118, 161). Such a character would be evidence of homoplasy and provides a phylogenetic definition of convergence. Therefore, identification of homoplasious characters is an additional potential method for defining adaptations. Variation in the patterns of homoplasy may be used for identification of antecedent conditions favoring trait transformation and for explaining why organisms show various levels of similarity. The evolutionary lability of characters may also be inferred by means of homoplasy (161, 162). Faith (44) used homoplasious characters in an ecological analysis of the Anseriformes. Similarity among species in the character space was inferred to represent convergence among phylogenetically dissimilar taxa that shared habitat and feeding preferences.

Phylogenetic Effects and Phylogenetic Constraints

A common goal among studies that include phylogenetic information in their analyses is to "control for the effects of phylogeny" in order to reveal the adaptive significance of a trait. This goal pervades comparative studies and spans many ecological and evolutionary analyses. Often, the explanations

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accompanying patterns of trait variation are painted in extremes of either adaptation or constraint. The attributes characterizing extant species are a mosaic of traits reflecting phylogenetic ancestry and independent changes that have accumulated since divergence from an ancestor. Many studies seek to partition variation in a trait that is independent of phylogeny to test hypotheses about adaptation (7, 21, 34, 37, 84, 113, 127, 179, 186, 188). Patterns of variation or covariation attributable to a legacy of phylogeny are invoked as evidence of phylogenetic constraint or inertia. However, in many studies phylogenetic effect is often confused with constraint or inertia. A definition of constraint is rarely presented, which renders it an ad hoc explanation rather than a testable prediction. Also, in the quest for testing adaptive hypotheses, the importance of phylogenetic explanations regarding the evolution of a trait is frequently ignored. A minimal condition for determining whether phylogenetic constraint applies to a particular trait is the demonstration of a phylogenetic effect (127).

It should be evident that phylogeny itself does not constrain nor does it affect the correlations among traits (118). Rather, the information embodied in a phylogeny has to do with changes in characters. Inferences about constraint should be derived from the patterns of trait transformation based on the phylogenetic tree. Any discussion of phylogenetic constraint should consider the following two points: First, an a priori definition of constraint would diminish the confusion that exists regarding the distinction between phylogenetic effect and phylogenetic constraint. Variation in a trait (or lack thereof) or the correlation of a trait with the hypothesized phylogeny of the in-group, i.e. lineage specific variation or covariation, is evidence of a phylogenetic effect (31, 37, 127). Constraint (or inertia) implies the restriction of the range of variation associated with a trait in response to fluctuations in the environment or changes in the selective milieu (37, 42, 72, 132). One must demonstrate that the diversification of a lineage or modification of a trait has been restricted during cladogenesis by limits in the rate of evolution, as evidenced by stasis, or in the pathways available for trait change (72, 118). How may phylogenies be used to identify constraint? We outline one possible protocol. First, identify regions of the phylogeny that lack high levels of character change, or where change is contingent on the presence of another character. This step provides evidence for a phylogenetic effect by establishing whether character changes are clustered or are contingent on the appearance of a second character (115, 118, 119). For example, in life history studies phylogenetic effects may be recognized by conservative patterns of variation within a clade (e.g. 37, 127). Second, trace the hypothesized shifts in the selective regime or environment on the phylogeny. The patterns of evolutionary stasis in the presence of hypothesized shifts in the environmental may be

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treated as evidence of constraint. Phylogenetic constraint as demonstrated by lineage specific variation may also be consistent with a number of processes that correlate with the diversification of a clade, for example, key innovations (see 37, 80, 82, 137).

The second point regarding phylogenetic constraint is the identification of the underlying causal mechanisms (80, 82, 136). In a comprehensive discussion of phylogenetic constraint, Edwards & Naeem (37) reviewed the processes consistent with patterns of character stasis in a phylogeny. Restricted variation in a trait may be attributable to (i) the inclusion of symplesiomorphies in the study, i.e. past adaptations that have become evolutionarily fixed, (ii) limited phenotypic variation, (iii) developmental canalization, (iv) phenotypic plasticity leading to the amelioration of strong selective regimes by the buffering of individuals from environmental fluctuation, (v) the absence of a selective shift (no change in the environment over time), or (vi) pleiotropy or the relatively rigid structure of the genetic variance-covariance matrix over evolutionary time (3, 37, 127). Phylogenetic constraints and the putative causal mechanisms should be considered only one of several alternative hypotheses about a character complex that is tested using a phylogeny. Determination of the mechanisms underlying the putative constraint remains a fertile endeavor for future comparative studies.

Areas In Ecology And Evolution That Have Used Phylogenetic Inference

Investigations in a myriad of fields in ecology, behavior, and evolution may be enriched by the use of information contained in phylogenetic hypotheses. Questions pertaining to cospeciation and coadaptation, such as might be predicted in insect-host or host-parasite interactions (4, 16, 48, 58, 128, 129, 173), the diversification clades and evolution of specialization (43, 46, 84, 92, 102, 132, 140, 149), chromosomal evolution (87), geographic variation (179), allometry (85, 157), heterochrony (10, 181) morphological evolution and innovations, (39, 59, 93, 105–107, 112, 157), the evolution of sexual dimorphism, social and mating systems (8, 9, 21, 40, 88, 130, 131, 134, 147, 150, 156, 174, 188), sexual selection (148, 189, 190), physiological ecology (12, 31, 38, 60, 62, 90, 142, 143, 184), evolution of life history traits (70, 82, 127, 141, 170, 171, 183, 195), the evolution of feeding behavior (77, 110, 151), community ecology (27, 29, 36, 104, 108, 109, 121, 139, 152, 154, 160, 164, 180, 194), behavioral ecology (16, 32, 56, 122, 125, 193), and conservation biology (16), are all amenable to hypothesis testing under an historical paradigm. This breadth in the types of studies employing phylogeny is mirrored by the diversity of methods devised by biologists who adopt an historical approach.

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A BRIEF SURVEY OF PHYLOGENY IN COMPARATIVE ANALYSES

However laudable and desirable, the capacity for phylogeny to inform various ecological or evolutionary studies ultimately depends on an analytical framework. The particular method employed will depend on the goals of the analysis, type of data (dichotomous, multistate, or continuous), and the information to be extracted from the phylogenetic tree. Presently, no fewer than seven methods that use phylogenetic information have been described in the literature (Table 1). Two broad classes of analyses are available: those that determine the direction of character change and those that remove the influence of phylogeny from the variation in a trait for testing adaptive scenarios (7, 16, 21, 52, 75, 90, 113). The former collection of methods is known as process-oriented analyses. These techniques are often implemented with data having discrete character states to reconstruct character evolution (159). The latter methods are appropriate for continuous characters, and in some circumstances multistate characters, when the goal is statistically to remove the influence of phylogeny or accomplish a partitioning of variation in a trait into phylogenetic and phylogeny-free components.

"Process-Theory" Methods

The methods that attempt to incorporate the information embedded in a phylogeny are extensions of cladistic methods or procedures that attempt to account fully for the topology of the phylogenetic hypothesis in analyzing character evolution (Table 1). Evolutionary models can be described in terms of a series of stages linking the initial state of a trait to a final state or evolutionary end point (20, 159). The expected transitional series defined under the evolutionary scenario may be compared directly to the patterns exhibited in the phylogeny. Three methods may be employed in testing process theories: (i) the mapping of characters onto a tree (character mapping via optimization methods), (ii) inferring the magnitude and direction of change in continuous characters by means of minimum evolution algorithms; (iii) derivation of a tree using the characters under investigation (i.e. life history, behavior, habitat associations, reproductive mode) and assessing the concordance of the trees by consensus methods.

CHARACTER MAPPING AND OPTIMIZATION Whereas the number of independent origins of a trait may be inferred using character mapping (126, 155), the testing of evolutionary models requires information about the character states for all internal nodes, or hypothetical ancestors. These estimates may be derived by optimizing the character onto the cladogram using parsimony methods (20). The procedure first requires establishing character polarity

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Table 1 A taxonomy of comparative methods and representative examples.

Method and source	Phylogenetic information	Representative studies
Methods for Removing or Controlling the Effects of Phylogeny		
Hierarchical (Nested) ANOVA (7, 24, 80)	Taxonomy	7, 34, 35, 79, 85, 177, 178
Phylogenetic autocorrelation (21)	Taxonomy, Phylogeny (Time since divergence from common ancestor, Genetic Distance)	8, 37, 65, 66, 127
Phylogenetic independent Contrasts (17, 52, 135)	Taxonomy, Phylogeny	27, 59, 62, 65, 81, 107, 130, 134, 139, 150, 152, 166, 170, 184
Phylogenetic regression (75, 76)	Taxonomy, Phylogeny	143, 183, 193
Phylogenetic pedigree (113)	Phylogeny	113
Methods for Inferring Correlated Change or Origin of Functional Complexes		
Minimum evolution (90) (Ancestor-Descendent Comparisons)	Phylogeny	37, 90, 107, 166, 184
Ridley's method of correlated change (Independent origins)	Phylogeny	56, 88, 91, 141, 147, 156
Character mapping and optimization (19, 25, 50, 126)	Phylogeny (Character transitions)	10, 12, 20, 33, 40, 58, 72, 87, 93, 123, 159
Sister group comparison (129)	Phylogeny	43, 46, 129, 131, 147, 190
Consensus methods (47)	Paired Phylogenetic trees	46

through outgroup analysis (e.g. 187). Next, under the assumption of parsimony, characters are mapped onto the tree such that the number of steps involved in the character transformation are minimized (33, 50, 87, 126, 174). However, there is considerable disagreement concerning the applicability of parsimony in reconstruction analyses (176). Also, character optimization may result in ambiguous estimates of the nodal character states, particularly if branch lengths differ (107, 111). The historical sequence of character state transitions (ancestral to derived) provide an estimate of the actual transformations contingent on the strength of the phylogenetic hypothesis upon which they are based. Character optimization methods have been applied in studies

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seeking to infer ancestral character states and the number of independent origins for a variety of traits, including sexual dimorphism in frogs (40), the evolution of the digestive tract in flies (93), heterochrony in the timing of cranial ossification in poeciliids (181), and the evolution of queen number in eusocial hymenoptera (12, 132). Hillis & Green (87) used character mapping to infer the number of independent origins of sex determination systems in amphibians. Their analysis revealed at least seven independent origins of male heterogamy. Furthermore, the phylogenetic analysis suggested a plausible model for the evolution of sex determination. A second use of character mapping is the determination of the sequence of character transitions in the phylogeny and their correlations with shifts in the selective regimes. The evolution of endothermy in fishes of the suborder Scombroidei is a recent example (12). Three independent origins of endothermy were detected after mapping the trait on a molecular phylogeny. Furthermore, each independent origin corresponded with an inferred niche shift into cold waters. Thus, the historical analysis suggested that endothermy in scombroid fishes represented an adaptation for expansion into cooler waters (12). Finally, the sequence of character changes may be used in transformational analyses that infer the origin of a feature and test hypotheses about evolutionary diversity or constraint (92, 100).

The association between dichotomous characters is also amenable to character mapping. Ridley (155) suggested entering the number of transitions into a contingency table and calculating the goodness of fit between the variables. Hoglund (88) was interested in determining the correlation between mating system and dimorphism in plumage characters among bird species. A minimum estimate of the number of independent origins for each character was determined by character optimization. Hoglund (88) applied Ridley's method and found that after considering the impact of phylogeny, lekking birds did not display greater amounts of dimorphism than did nonlekking birds. However, this method ignores the sequence of transitions, that is, whether a shift in mating system precedes the evolution of size dimorphism or vice versa. Few applications of Ridley's method have discussed this weakness (but see 115, 173, 174). An alternative question is whether the change in one character is associated with change in another more often than expected by chance. For example, questions about the evolution of mating systems may be expanded to ask whether polygyny has evolved more often in dimorphic lineages than in monomorphic lineages.

MINIMUM EVOLUTIONARY METHODS AND HISTORICAL TRANSFORMATION A useful extension of character mapping in comparative analysis is tracing the amount of change in successive ancestor-descendant comparisons using continuous rather than discrete characters. Minimum evolution methods

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attempt to reconstruct the values of each variable for all interior nodes, i.e. hypothetical ancestors, assuming a particular model of evolution. Subsequent comparisons between the ancestor and descendant taxa are used to elucidate the direction of character change and its magnitude. Historical transformation analyses proceed by comparing the rates of change for two or more variables using correlation or multivariate methods (89, 107, 184). The reconstruction of the ancestral values may be accomplished through two techniques. One common method, linear or Wagner parsimony, estimates character states by calculating the median value of the three nearest nodes, such that the total amount of change in the whole tree is minimized (50, 182). A weakness with this method is that a range of equally parsimonious values is often estimated for each branch (118). Only when a tree is fully resolved will this method produce a unique solution. An alternative procedure, squared change parsimony, does not exhibit this weakness and has been a preferred approach (89, 107). Here, the quantity minimized is the sum of squared change in each branch of a tree, summed over all branches (107, 116). The squared change parsimony model is partly based on a method of minimum evolution and yields a Bayesian probability estimate of ancestral character states under a brownian motion model of evolution (116). However, it is an empirical model that provides the best fit to a data set and as such represents a method rooted in analytical convenience rather than any model of the evolutionary process (107, 111; Miles & Dunham, manuscript in preparation).

Comparative studies based on ancestor-descendant comparisons are directly applicable to expediting the transformational approach toward establishing the historical pathways of character change and covariation (92, 97). Walton (184) applied a transformational approach to an analysis of the evolution of locomotory energetics in hylid frogs. The analysis revealed a presumed evolutionary shift in activity metabolism from the inferred low rates of neotropical ancestors to the high rates of extant temperate taxa. Other applications include the evolution of ecomorphological relationships (107) and reconstruction of avian group size among cooperatively breeding birds (37). While the estimation of character change between ancestor-descendant species pairs is straightforward, the use of parametric statistical procedures evaluating the patterns may be problematic for two reasons. First, the change along successive branches is not independent of change in earlier branches (107). Second, a sample of n tip species yields $2n$–2 ancestor-descendant comparisons, which inflates the sample size (107). Therefore, inferential statistical procedures may have to use resampling or simulation methods for determining the actual significance levels (120).

SISTER GROUP COMPARISONS Identifying the underlying features or phenotypic traits affecting evolutionary rates and diversification of lineages is a

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central goal of evolutionary biology. One possible explanation is a causal link between the appearance of a "novel phenotypic innovation" or "key adaptation" and the subsequent radiation of the lineage (92, 101, 105). Because the hypothesized "key innovation" evolved only once, explicit tests of key adaptations were hampered by the absence of a methodology that could identify the novel trait characterizing the diverse lineage and select the appropriate clade for comparison. Lauder and associates (100, 101) advocated sister group comparisons to determine the adaptive significance of functional complexes in morphological studies. Ecologists have also utilized sister-group comparisons to investigate the hypothesis that a novel trait was associated with the diversification of a clade.

The procedure consists of three steps: First, completely specify all monophyletic groups that have independently evolved the novel trait. Second, determine the sister groups that lack the trait. Third, compare patterns of species richness, ecological breadth, or other measure of diversification between the sister groups (46, 92, 101, 129). The procedure can be repeated among different clades to assess the historical repeatability of the key innovation. There are many examples of sister group comparisons in the literature. Using sister group comparisons, Mitter et al (129) demonstrated that phytophagous insect lineages had greater numbers of species than the immediate sister group that fed on prey items other than plants. Sister taxa comparisons were used to assess the correlation between flight design and mating system in butterflys (190). Other applications include determining the association between mating system and parasite load in passerine birds (147) and evaluating historical patterns of character change in frog pectoral girdles (39).

CONSENSUS METHODS An underexploited procedure for comparative analyses involves the direct comparison of cladograms to provide evidence of phylogenetic concordance between the structure of two or more independent data sets. Consensus methods comprise a set of procedures that are useful for comparing cladograms derived from different data sets measured on the same taxa. A useful application of consensus methods would involve testing the hypothesis of parallel diversification between insects and their host plants (46). Evidence of parallel diversification would be suggested by the similarity in topology of the insect and plant phylogenies. Generally, consensus procedures produce a single tree by seeking the common groupings between cladograms. The similarity among two or more trees is ascertained by the resolution given in the consensus tree (16, 47, 118). One measure of consensus resolution is provided using either a weighted or unweighted "simple consensus fork index," which is a measure of the total number of groups found relative to the greatest number of groups possible (47). Significance

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levels associated with the fork index may be derived by using the Monte Carlo distributions derived by Shao & Rohlf (167) and Shao & Sokal (168).

Statistical Methods for Controlling the Influence of Phylogeny

The following comparative methods seek to control for the influence of phylogeny when analyzing quantitative traits. By far, these methods are the most extensively used by ecologists and evolutionary biologists. Presently, there are five general methods for incorporating phylogenetic information in statistical analyses: (i) hierarchical (nested) ANOVA models; (ii) Lynch's phylogenetic pedigree model; (iii) phylogenetic autocorrelation; (iv) independent contrasts; and (v) the phylogenetic regression. Because earlier reviews have elaborated on the mathematical properties of these methods (61, 67, 68, 80, 82, 136), we restrict our discussion to the potential uses of the methods.

Early comparative studies that sought to remove the influence of phylogeny prior to evaluating the adaptive significance of a trait, especially in life history analyses, applied Nested Analysis of Variance models (7, 23, 24, 34, 35, 79, 177, 178). Phylogenetic relationships were estimated by using the taxonomic categories for the group of species included in the study. An outcome of Nested ANOVA models was the partitioning of variation in a trait among the various taxonomic levels, e.g. order, suborder, family, genera, etc. The taxonomic category associated with the greatest amount of variance was considered to carry most of the influence of phylogeny (24, 85, 136). Subsequent analyses based on a higher taxonomic level were assumed to be free of phylogenetic effects and hence explained adaptive trends in character variation (24, 80). The reliance on a taxonomic classification rather than a phylogenetic tree in the use of a Nested ANOVA represents at best an indirect approach to eliminate the influence of phylogeny. Instead of explicitly using the branching sequence of a tree to express the relationships of the constituent taxa, ANOVA models circumvent and reduce the problem of confounding of variation due to phylogeny. Care must be taken to ensure correct classification of the taxa, for errors in the taxonomy can lead to biased results (compare 34 and 178). Consequently, these models are not recommended for controlling the influence of phylogeny.

Lynch's pedigree model (113) is a versatile procedure that has been used infrequently. Lynch's method is germane for comparative analyses with the goal of measuring the strength of phylogenetic effects, controlling for the influence of phylogeny, estimating ancestral character states, and hypothesis testing of the derived estimates. A particular advantage of the procedure is the capacity to simultaneously analyze many variables and generate estimates of phylogenetic covariation among the traits. Lynch (113) extended the application of mixed model methods developed in animal breeding studies to the problem of incorporating phylogeny in comparative studies. In this

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method, the total variation in a trait is partitioned into a "heritable additive component," a grand mean for the whole phylogeny, and a residual component. Phylogenetic information is included in the analysis by a matrix "**G**" that contains the measures of phylogenetic relatedness, estimated by the time since divergence from a common ancestor or branch lengths. The method has several appealing features: minimization of bias in the estimates of ancestral character states due to independent evolution in the tip species since divergence from a common ancestor, partitioning of variation that is taxon specific and related to microevolutionary processes, and variation that is attributable to phylogeny and macroevolutionary pattern. Although initial analyses appear quite promising, so far, the method has yet to be extensively applied.

The remaining three comparative methods are available as microcomputer programs; consequently, these have been more widely applied. One method, phylogenetic autocorrelation, may be used when the goal of the analysis is to assess the correlation between a trait and the phylogenetic hypothesis, i.e. elucidation of phylogenetic effects, and to obtain specific trait values for each species that is free of phylogeny (21, 37, 67, 127). Based on spatial statistics models, the phylogenetic autocorrelation was derived to estimate the strength of phylogenetic inertia in a trait (21). Also, the magnitude of the squared autocorrelation coefficient estimates the degree to which variation in a trait is explained by phylogeny. For example, in a study of life history variation among iguanid reptiles, Miles & Dunham (127) found significant phylogenetic correlations for age at maturity, mean adult female body size, and neonate size, with the amount of variation explained by phylogeny varying between 36% and 51%. The methods' principal advantage is the partitioning of total trait variation into two components, one describing phylogenetic values or inheritance from ancestral taxa, and a specific value that pertains to independent evolution since divergence from a common ancestor. Users of the method should be aware that the method factors any covariation between the phylogenetic and specific values into the phylogenetic component of trait variation (21). Only the specific values are pertinent to the testing of hypotheses of adaptive scenarios (8, 21, 127).

One critique of phylogenetic autocorrelation concerned the use of taxonomic distance as an estimate of phylogeny (48, 69, 100). Phylogenetic information is entered into the analysis via a general weighting matrix (the phylogenetic connectivity matrix, **W**). The magnitude of the autocorrelation coefficient will depend on **W**, so it is essential that accurate phylogenetic information is available. Yet, few data are available about the impact of error in the weighting matrix on the autocorrelation estimate (see 21 and 80). In the description of the method, Cheverud et al (21) used a taxonomic measure of similarity, but proposed several alternative weighting schemes. The only limitation of the

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weights is the requirement to describe the descending levels of relatedness by any monotonically declining function. Miles & Dunham (127) rejected the use of taxonomic distances and instead used a measure of phylogenetic distance similar to the patristic distance developed by Farris (50; see also 70). Gittleman & Kot (66) extended the method by including an additional undetermined, exponential factor to the phylogenetic weights. The exponent, designated α and estimated by maximum likelihood procedures, adjusts the phylogenetic distances to account for differences in branch lengths between pairs of ancestor-descendant taxa. Thus, tremendous flexibility exists for estimating the elements of the phylogenetic connectivity matrix, **W**. A variety of modifications other than α may be introduced to accommodate variations in phylogenetic information (see 22). Any index that describes the hierarchical nature of relatedness among species as portrayed in a phylogeny may be employed, e.g. genetic distances, differences between species in mitochondrial DNA sequences (e.g. 37), branch lengths, or time since divergence.

Two additional methods have been derived that apply the phylogenetically independent contrasts approach proposed by Felsenstein (52, 54). Briefly, if differences in the value of a trait are generated between sister taxa or nodes, then the values will be free of phylogenetic effects. Contrasts are independently calculated for two or more variables (with the sign arbitrary) and then used in subsequent correlation or regression analyses. Although the method does not necessarily result in generating evolutionary sequences of character change, it has been applied in those studies seeking a correlation between two traits that is free of the influence of phylogeny. For example, morphology and foraging behavior are known to be correlated in birds (152, 154). Similar species may forage in a similar manner because of common ancestry. Therefore, ecomorphological correlations among related species of birds may reflect the influence of phylogeny. What is the correlation between morphology and ecology after adjusting for phylogeny (152)? Given a well-corroborated phylogeny, estimates of the branch lengths and the character states of the extant taxa for two variables, the contrasts method constructs a series of independent comparisons along successive bifurcations along the branches of the tree. Because sister taxa are of equal age, the contrasts are independent of phylogeny. Richman & Price (152) found that among-species' variation in several ecological attributes, such as prey size, and foraging technique, was strongly correlated with morphology, after removing the effects of phylogeny.

The two versions of independent contrasts are different implementations of Felsenstein's original method and differ in the underlying statistical model and method for generating the contrasts (75, 82, 135). Each has also modified Felsenstein's model to accommodate the ambiguous nature of unresolved polytomies (75, 80). Despite their overt similarity, some disagreement exists over the superiority of a given method (76, 138). The heart of the differences

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appears to be the manner in which branch lengths are used, the resolution of polytomies and decision of whether to use a weighted regression (76, 135). Both employ nonphylogenetic methods for resolving polytomies. In Harvey & Pagel's model (80), the mean character state is calculated, and the trait values of the member taxa are standardized against the group mean; taxa most similar in the mean values are assumed to be closely related. Hence, the polytomy is resolved by the successive agglomeration of taxa most similar in the value of the trait under investigation. Grafen (76) derives linear contrasts based on the deviation of descendant taxa from the mean value of the parent node.

However, potential users of independent contrasts should realize this method makes several stringent assumptions. First, character evolution may be modeled by brownian motion (52, 54, 120, 137). Second, if the phylogeny was generated using molecular data, then one must assume some form of molecular clock to derive estimates for the branch lengths. The availability of branch lengths allows one to calculate an expected variance of a trait. Under the model of brownian motion this turns out to be proportional to time. If the brownian motion model of character evolution is incorrect, then the contrasts are no longer independent of phylogeny (52, 111). As outlined by Felsenstein (54), the model also assumes the availability of a known phylogeny. However, many recent applications have used the contrast method with taxonomies, i.e. no topological information, in place of phylogenies (11, 130, 150). Finally, for the purposes of meeting the assumptions of parametric statistics, each contrast must be standardized by the standard deviation of the branch lengths. Without information on branch lengths, all branches may be assumed to be of equal length. While contrasts that are derived using branch length data are said to represent a gradual model of character evolution, those made under the assumption of equal length of branches are argued to represent punctuational change (61, 82, 120, 137). The availability of branch lengths does not necessarily mean that character change is gradual. Such assertions concerning the mode of evolution should be tested (e.g. 102).

One implementation of the contrast method does not require the availability of branch lengths and may be used in studies where the assumptions cannot be met (17). Because contrasts are determined at each bifurcation, the character values at each node should be of equal age, and the need for standardization by branch length is superfluous (111). Standardization also means that information about absolute change is lost; rather, evolutionary change is expressed as change per unit standardization (107, 111). Finally the correlations derived from independent contrasts may be affected by several factors. Correcting for varying branch lengths may inflate the correlation between traits. Suppose two traits change early in the phylogeny, but remain relatively static at the terminal branches. Because the branches may differ in

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length, standardization of both characters by branch length may result in a correlation when little or no change has occurred (111, 118). Contrasts based on phylogenetic trees with high levels of homoplasy may lead to inflated correlations (26). Unfortunately, little information is available concerning the efficacy of the method with varying levels of homoplasy in phylogenetic trees.

A Comparison of Comparative Methods

Given the diversity of comparative methods, what is the best comparative method for including phylogeny in ecological and evolutionary studies, and does the choice make a difference in one's interpretation of the patterns embedded in the data? Unfortunately, very few studies incorporate more than a single phylogenetic hypothesis and comparative method in the analysis. Of the few studies that employed alternative phylogenies, most reported consistent results in the subsequent statistical analyses (e.g. 66, 127, 173). Sillén-Tullberg and Møller (173) found no changes in the number of transitions in ovulatory signs in anthropoid primates, but they did find an additional transition in mating system when they employed a second alternative phylogeny of the Cercopithecoidea. Because the available methods often have different goals, some differences in the results may be expected. The few studies that employed more than one comparative method found little difference in the results. Statistical analyses based on phylogenetic independent contrasts and minimum evolution methods converged on similar conclusions (e.g. 107, 184). Similar results were also reported in an analysis of carnivore olfactory bulb size where both independent contrasts and phylogenetic autocorrelations were used (65).

Evidence of disagreement has also appeared. The results from a Nested ANOVA model differed sharply with those obtained from the autocorrelation analysis of lizard life history traits (127). The proportion of variance in several life history traits was higher using the nested ANOVA than that found by phylogenetic autocorrelations. A reanalysis of Hoglund's (88) study on the association between plumage dimorphism and lekking behavior in birds using independent contrasts found a significant correlation (134). The difference in conclusions may be a consequence of coding a continuous trait (actual sexual size dimorphism) into a discrete character (presence or absence of size dimorphism) for the purposes of using Ridley's method of analysis as well as other factors, such as the nonindependence of successive ancestor-descendant comparisons (134; see also 1 for coding continuous characters.).

Can a particular comparative method be recommended for a specific type of analysis? The method used by a biologist depends on the question and the type of data. In a recent analysis, Edwards & Naeem (37) used three different methods to describe the role of phylogeny in the evolution of cooperative breeding in birds. First, the number of origins and ecological correlates of

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cooperative breeding were inferred using character mapping. Next, the evolutionary shift in mean group size was estimated using ancestor reconstruction methods. Lastly, the proportion of variation in group size attributable to phylogeny was derived using the method of phylogenetic autocorrelations. Future comparative studies may require several methods for unraveling the imprint of history in the expression of a character.

Computer simulations provide one promising pathway for evaluating the performance of the various comparative methods. Recent simulation studies discussed the performance of several comparative methods often using different estimates of phylogenetic relatedness (60, 67, 68, 120). Their results indicated that levels of type 1 and type 2 error are contingent on the method used (e.g. contrasts versus minimum evolution, or autocorrelation), model of character evolution (gradual versus punctuational), and sample size (67). While the simulations demonstrate the ability of these methods to incorporate phylogeny, the statistical power of the tests is an under appreciated problem that requires additional investigation (120).

EVALUATION OF PHYLOGENETIC HYPOTHESES

Choosing a Well-Corroborated Phylogeny

All recent comparative methods assume the availability of a well-supported phylogeny (16, 33, 52, 80). The problem remains of how to select the best supported phylogenetic hypothesis when more than one tree (phylogenetic hypothesis) is available. Such situations arise when a single data set yields multiple equally parsimonious trees, or when different trees were derived from independent data sets.

Two points are critical: first, phylogenetic trees are *hypotheses* of genealogical relationships of the taxa given the characters and their patterns of transition. The outcome of a comparative analysis is contingent on the resolution of the phylogenetic tree. Thus, as additional information about the phylogenetic relationships of a clade appears (e.g. resolution of polytomies), the results of previous comparative studies may have to be reevaluated (e.g. 62 and 90). Second, the polarity of character states and the structure of the tree depend on choice of outgroup. Thus, the topology (and hence estimates of phylogenetic relationships among taxa) of the tree may be affected by the addition or deletion of taxa or characters (95, 122, 133) as well as by the method used to generate the tree (158). Although equally parsimonious trees may not differ in length (number of required character transitions), they may vary in the topology. Differences in tree topology will affect the conclusions about character state transformations and the inferences of evolutionary patterns based on among species comparisons (4, 16, 20, 33, 58, 118, 122).

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Among possible phylogenetic hypotheses, which tree will provide the most accurate information regarding the history of the focal group?

The criteria for evaluating different trees have been the subject of intense interest in the phylogenetic systematic literature (e.g. 19, 45, 69, 118, 191, 192). However, recent reviews of comparative methods largely ignore discussion of the criteria necessary to choose among different trees (80, 82). Also, many of the new comparative techniques require a well corroborated phylogeny, but few of the studies employing these methods discuss the criteria used in selecting a hypothesis given multiple possible alternatives, which suggests the decision was arbitrary (71, 130, 149, 183). Strongest evidence of a well corroborated phylogeny is the generation of similar topologies from independent data sets (16, 95, 158, 186, 192). In the absence of alternative hypotheses based on independent data sets, other criteria must be employed.

The most commonly employed criterion is the consistency index (CI), which describes the ratio of the minimum number of changes per number of characters to the actual number of transitions. The congruence of the characters with the cladogram is summarized by the consistency index, which is also interpreted to represent levels of homoplasy. The CI varies between 1.0 (complete agreement of the characters with the topology) to 0.0 (complete homoplasy). Generally, the phylogenetic hypothesis best supported by the data will have a high CI. In evaluating consistency indices from a number of trees, it should be taken into account that the CI will be inflated by invariant and autapomorphic characters. While the consistency index has been the most prevalent measure because of its simple derivation and ease of interpretation, other indices are available that measure the amount of homoplasy in the tree; these include the retention index, homoplasy slope ratio, and homoplasy excess ratio. However, these indices are sensitive to the number of characters and taxa included in the analysis, which may influence the choice of a phylogeny (16, 94, 162, 192).

A phylogenetic reconstruction that results in the generation of a large number of equally parsimonious trees suggests that the set of available characters does not strongly support any totally resolved phylogeny (118). A compromise tree is often derived using consensus methods, which attempt to aggregate the common groupings among different cladograms (95, 192). Originally intended to allow comparisons of cladograms derived from different character sets, it is often used to produce a summary tree. Generally, the resulting consensus tree will be less resolved (have more unresolved polytomies) than any of the original cladograms (19). An alternative method for choosing among phylogenies was described by Carpenter (19), who proposed that the application of "successive approximations character weighting." Other methods such as randomization procedures (e.g. 45) or data decisiveness indices (69) may also be used for choosing among multiple phylogenies.

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Possible Biases in Phylogenies

Biologists interested in employing recent comparative methods should be aware of the possible biases accompanying the analysis of character evolution using phylogenies (16, 80, 120). These include the independence of the phylogeny from the data to be analyzed, the influence of missing taxa, elimination of characters from the phylogenetic analysis, errors in the phylogeny, and completeness of the ecological data (4, 16, 49). Another under-appreciated bias involves the correct coding of characters (125).

A topic of some controversy involves whether to include characters used to construct the phylogeny in the comparative analysis. Most studies recommend that reconstruction of a phylogeny employ characters independent of the ecological or evolutionary traits to be analyzed (4, 16, 82, 100, 101, 174). However, several systematists argue that all the available evidence should be used to reconstruct a phylogeny (e.g. 95). To do so will result in a conservative estimate of the number of independent origins of a trait. Consider a trait, say, mode of reproduction in lizards, that was used in both the analysis and the phylogenetic tree. Because most trees are generated under the principle of parsimony, the number of evolutionary transitions in the trait will be minimized within the phylogeny.

The results from comparative methods depend on the topology of the cladogram, and evidence suggests that the topology may change with the addition or deletion of characters or species (16, 95). Should the branching sequence change, then interpretations about the origin of a trait and its adaptive significance may be modified (4, 16, 117, 133). Consequently, as many species as possible should be included in the phylogenetic reconstruction (16, 124), and the stability or confidence of the bifurcations (nodal taxa) using resampling methods such as the bootstrap should be evaluated (e.g. 53). Not all cladograms may be fully resolved (i.e. dichotomous branching at every node); at some nodes the genealogical relationships among the constituent taxa are ambiguous given the available data, and this results in polytomies. Potential explanations for polytomies include: (i) the characters included in the analysis are uninformative with respect to this particular group of taxa (soft polytomies), and (ii) the existence of a multiple speciation event (hard polytomies). Methods for resolving polytomies vary depending on their interpretation (see 114 and 144).

Finally, the interpretation of evolutionary scenarios is often accomplished using character optimization (50, 58). Incomplete ecological data will affect character alternatives and often arrive at ambiguities in the determination of ancestral character states and unresolvable interpretations about the evolution of trait complexes (e.g. 4). Also, comparative analyses are based on the assumption that the traits are homologous (125). McLennan & Brooks (125)

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discussed the need for increased precision by ecologists in defining ecological and behavioral characters to meet this assumption prior to performing the analysis. The use of nonhomologous traits may vitiate any attempts at unravelling the ecological features associated with the evolution of a character (125).

Why Not Use Taxonomic Classifications

The rising popularity of comparative methods has created an increased demand for phylogenies from a variety of taxa. In many cases, a well corroborated phylogeny is not available, and biologists will use a taxonomic classification. Taxonomies may not be a suitable alternative for a well corroborated phylogeny for several reasons (122). The hypothesis of relationships as depicted in a Linnean taxonomy may not have been constructed using recent cladistic methods, and so it does not necessarily portray the ancestor-descendant relationships or branching patterns that are described by phylogenies (145). Also, the hierarchical structure of the classification may not reflect the true patterns of phylogeny. Hence the various taxonomic categories of equal rank may be of equivalent age and not necessarily sister taxa (see 145, 146). In the absence of the structure of a tree, it is difficult to estimate the sequence and direction of character change. Finally, taxonomic categories are not always monophyletic groups; they may be comprised of paraphyletic or polyphyletic groups. Consider a trait that evolved only once prior to the diversification of a clade, but the descendant taxa of which current classification schemes incorrectly place into different families. The number of independent origins of the trait will be incorrectly inferred, should the analysis proceed at the family level.

In light of these weaknesses, within a group of closely related species, it is difficult to have much confidence in interpreting the number of origins of a trait based on a classification. There are instances where classifications are suitable for inferring the number of independent origins of a trait, e.g. evolution of flight in birds and insects. Substituting classifications for a phylogeny may bias those comparative procedures based on sister-group comparisons or phylogenetically independent contrasts. First, the uncertainty of monophyly at various taxonomic ranks will artificially inflate the number of independent origins of a trait and tend to erroneously favor hypotheses of adaptation. Second, although independent contrasts may be calculated using various taxonomic ranks, the assumption of equal age may incorrect. Consequently, the analysis may reject a hypothesis of historical effects in favor of an adaptive explanation. The use of classifications in comparative analyses is a complex issue. Recent advances in phylogenetic taxonomy may clarify the ambiguities surrounding the use of classifications. Because most of the early classifications may not have been developed using a phylogenetic

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methodology, the translation of taxonomic categories into phylogenetic trees and secondarily used to deduce branch lengths, as suggested by several authors (61, 67, 75, 80), may be premature (16).

SUMMARY

In view of the rapid expansion of comparative analyses, a major question is, which method is appropriate for which particular analysis? Because of the diversity of methods currently available, such a question is not trivial. The manner in which a phylogeny is incorporated into a comparative method depends entirely on the ecological and evolutionary contexts of the study and the type of hypothesis to be tested. Inclusion of a phylogenetic perspective in ecological and evolutionary analyses has the potential to refine our hypotheses and suggest new analyses to test redefined problems. However, the uncritical application of historical methods without reference to evaluating the quality of the phylogenetic hypothesis or to evaluating the underlying assumptions diminishes the power of the analysis (125).

An historical perspective provides the framework from which to establish the sequence of character changes that describe complex behavioral, ecological, or evolutionary patterns. Thus, the new comparative methods should be considered a breakthrough rather than a burden. Phylogenetic hypotheses represent our best estimate or reconstruction of genealogies and character state transformation for extant taxa. As such, they embody patterns of macroevolutionary change. These patterns may suggest appropriate experiments or observational studies at a microevolutionary level (e.g. 122, 124). Furthermore, the historical methods complement and enhance explanations of contemporary patterns (165). For a variety of reasons, classifications are not adequate substitutes for phylogenies (125). This does not mean that biologists must now become cladists, but it does suggest that a comparative method requires more effort than simply picking up a classification and executing an autocorrelation or independent contrasts analysis. Biologists must carefully consider recent phylogenetic analysis and evaluate the strength of the genealogical hypothesis.

The inclusion of phylogeny in ecological and evolutionary analyses augments our interpretations of the diversity of life. We argue that the addition of phylogeny in ecological analyses provides a formal null model for adaptations and can suggest appropriate comparisons for testing adaptive hypotheses. Although removing the influence of phylogeny in comparative analyses is a laudable goal for understanding variation or covariation among traits, the historical component in trait variation provides insights into the origin of adaptive traits. Because of the potential biases inherent in the use of phylogenies, we suggest that caution is necessary in applying phylogenies

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to comparative analyses. Finally, new applications of phylogenetic information in ecology and evolution are occurring rapidly. We propose that the current emphasis on removing phylogenetic effects in comparative analyses should shift to one of directly using the phylogeny to make explicit predictions about character change that are amenable to experimental manipulation or field observation. Such studies have already been published and demonstrate the feasibility of such an approach.

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